Hopf Bifurcation in a Model for Biological Control

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Abstract

In this paper we study the Lyapunov stability and Hopf bifurcation in a biological system which models the biological control of parasites of orange plantations.

Key-words: Hopf bifurcation, stability, periodic orbit, biological control.
MSC: 70K50, 70K20.

1 Introduction of the Mathematical Model

In this work we study a system of four coupled differential equations (1) which models the interaction between two biological species, each presenting two stages in their metamorphosis, living in a common habitat with limited resources.

The differential equations analyzed here are

$$\begin{aligned}
P' &= \frac{dP}{dt} = \phi_1 \left(1 - \frac{M}{c_1}\right) M - (\alpha_1 + \beta_1)P - k_1 PG \\
M' &= \frac{dM}{dt} = \alpha_1 P - \mu_1 M \\
L' &= \frac{dL}{dt} = \phi_2 \left(1 - \frac{G}{c_2}\right) G - (\alpha_2 + \beta_2)L + k_2 PG \\
G' &= \frac{dG}{dt} = \alpha_2 L - \mu_2 G.
\end{aligned} \tag{1}$$

This model —an elaboration of Lotka-Volterra equations, taking into account the stages or compartments in the biological populations— was proposed by Yang and Ternes [1, 2] and Ternes [3] for a study of the biological control[1] of orange plantations leaf parasites P, which is a pre-adult stage for M, by their natural enemies L, which is an early stage for G.

Other differential equations have been proposed as models for interacting populations partitioned in compartments, representing several situations of biological interest. See, among many others, Hethcote et al. [4], Jacquez and Simon [5] and Godfray and Waage [6].

In [1, 2] and [3] P and M are the densities of pupae[2] and female adults of *Phyllocnistis citrella* (which in its larva[3] stage is the citrus leafminer[4]), L and G are the densities of larvae and female adults of its native parasitoid

[1] http://en.wikipedia.org/wiki/Biological_control
[2] http://en.wikipedia.org/wiki/Pupa
[3] http://en.wikipedia.org/wiki/Larva
[4] http://www.agrobyte.com.br/minadora.htm; http://en.wikipedia.org/wiki/Citrus

Galeopsomyia fausta (whose larvae feed on the pupae of M[5]).

The meaning of the parameters in (1), where the notation of [1, 3] has been preserved, is as follows: α_1 is the rate of pupae that give rise to adults M, β_1 is the mortality rate of pupae, μ_1 is the mortality rate of adults M, ϕ_1 is the rate of eggs that give rise to pupae, c_1 is the carrying capacity of the population M, α_2 is the rate of larvae that, evolving through pupae, give rise to adults G, β_2 is the mortality rate of larvae and pupae, μ_2 is the rate of mortality of adults G, ϕ_2 is the oviposition[6] rate of the parasite and c_2 is the carrying capacity of the population G. Here we assume that the pupa (respectively larva) population decreases (respectively increases) at a rate proportional to $P - G$ encounters that is $k_1 PG$ (respectively $k_2 PG$).

This model represents the evolution of female populations. If necessary the male populations can be estimated using the sexual ratio of each species.

Remark 1.1 *All the parameters* $\alpha_1, \beta_1, \mu_1, \phi_1, c_1, k_1, \alpha_2, \beta_2, \mu_2, \phi_2, c_2, k_2$ *are positive. As the damage to the* P *population must be larger than the benefit to the* L *population it is natural to assume that* $k_1 \geq k_2$.

Here will be established the location and the stability character of the equilibria of (1), four in number. Also is determined the bifurcation variety in the space of parameters, representing the transition from asymptotically stable to saddle type at the equilibrium point with positive coordinates, representing the coexistence of the two species. See Theorem 2.4 and its Corollary 2.5.

Fixing the all the parameters in (1) to biologically feasible values, taken from [3] and [7], but letting the interaction coefficients k_1 and k_2 vary in a positive quadrant, the nature of the bifurcation phenomenon in this plane by crossing the bifurcation curve is established. See Theorem 3.1 and Figure 1. This is done by means of a computer assisted calculation of the first

[5]http://www.seea.es/conlupa/AlbertoWeb/framesparasitoides.htm. This site has impressive photos of hosts and parasitoids.

[6]en.wikipedia.org/wiki/Oviposition

Lyapunov coefficient, found to be positive. The Hopf bifurcation analysis of this point implies that the bifurcating periodic orbit is asymptotically unstable, of saddle type which surrounds an attracting equilibrium with small attracting basin. The dependence of the bifurcation curve on the parameter c_2 is studied in Theorem 3.3 and illustrated in Figure 3.

In Section 4 the implications of the results in this paper are discussed and interpreted from a wider perspective.

2 Stability Analysis of Equilibria

Assume the following notation:

$$R_1 = \frac{\alpha_1\phi_1}{\mu_1(\alpha_1+\beta_1)}, \;\; R_2 = \frac{\alpha_2\phi_2}{\mu_2(\alpha_2+\beta_2)}. \tag{2}$$

The differential equations (1) have four equilibria

$$\mathcal{A}_1 = (P_1, M_1, L_1, G_1) = (0,0,0,0), \tag{3}$$

$$\mathcal{A}_2 = (P_2, M_2, L_2, G_2) = \left(\frac{c_1\mu_1}{\alpha_1}\left(1-\frac{1}{R_1}\right), c_1\left(1-\frac{1}{R_1}\right), 0, 0\right), \tag{4}$$

$$\mathcal{A}_3 = (P_3, M_3, L_3, G_3) = \left(0, 0, \frac{c_2\mu_2}{\alpha_2}\left(1-\frac{1}{R_2}\right), c_2\left(1-\frac{1}{R_2}\right)\right), \tag{5}$$

and

$$\mathcal{A}_4 = (P_4, M_4, L_4, G_4), \tag{6}$$

where

$$P_4 = \frac{c_1\mu_1\phi_2}{\alpha_1^2\phi_1\phi_2+\mu_1^2c_1c_2k_1k_2}\left(\alpha_1\phi_1\left(1-\frac{1}{R_1}\right)-\mu_1c_2k_1\left(1-\frac{1}{R_2}\right)\right),$$

$$M_4 = \frac{c_1\alpha_1\phi_2}{\alpha_1^2\phi_1\phi_2+\mu_1^2c_1c_2k_1k_2}\left(\alpha_1\phi_1\left(1-\frac{1}{R_1}\right)-\mu_1c_2k_1\left(1-\frac{1}{R_2}\right)\right),$$

$$L_4 = \frac{c_2\mu_2\alpha_1\phi_1}{\alpha_2(\alpha_1^2\phi_1\phi_2+\mu_1^2c_1c_2k_1k_2)}\left(c_1\mu_1k_2\left(1-\frac{1}{R_1}\right)+\alpha_1\phi_2\left(1-\frac{1}{R_2}\right)\right),$$

$$G_4 = \frac{c_2\alpha_1\phi_1}{\alpha_1^2\phi_1\phi_2+\mu_1^2c_1c_2k_1k_2}\left(c_1\mu_1k_2\left(1-\frac{1}{R_1}\right)+\alpha_1\phi_2\left(1-\frac{1}{R_2}\right)\right).$$

Remark 2.1 *If $R_1 > 1$ and $R_2 > 1$, then the equilibria $\mathcal{A}_1$, $\mathcal{A}_2$ and $\mathcal{A}_3$, have only non-negative coordinates. If $k_1 < k_{1_{max}}$, where*

$$k_{1_{max}} = \frac{\alpha_1 \phi_1 \left(1 - \frac{1}{R_1}\right)}{c_2 \mu_1 \left(1 - \frac{1}{R_2}\right)}, \tag{7}$$

then the coordinates of the equilibrium $\mathcal{A}_4$ are also non-negative.

The Jacobian matrix of (1) at $\mathbf{x} = (P, M, L, G) \in \mathbb{R}^4$ has the form

$$J(\mathbf{x}) = \begin{pmatrix} -\alpha_1 - \beta_1 - k_1 G & \phi_1 - \frac{2\phi_1 M}{c_1} & 0 & -k_1 P \\ \alpha_1 & -\mu_1 & 0 & 0 \\ k_2 G & 0 & -\alpha_2 - \beta_2 & \phi_2 - \frac{2\phi_2 G}{c_2} + k_2 P \\ 0 & 0 & \alpha_2 & -\mu_2 \end{pmatrix}, \tag{8}$$

while its characteristic polynomial is given by

$$p(\lambda) = det(J(\mathbf{x}) - \lambda I) = \Theta_1 \, \Theta_2 + \alpha_2(\mu_1 + \lambda) k_1 k_2 P G, \tag{9}$$

where

$$\Theta_1 = (\mu_1 + \lambda)(\alpha_1 + \beta_1 + k_1 G + \lambda) - \alpha_1 \left(\phi_1 - \frac{2\phi_1 M}{c_1}\right)$$

and

$$\Theta_2 = (\mu_2 + \lambda)(\alpha_2 + \beta_2 + \lambda) - \alpha_2 \left(\phi_2 - \frac{2\phi_2 G}{c_2} + k_2 P\right).$$

Recall that an equilibrium point $\mathbf{x_0}$ is said to be a *saddle of type* $n - p$ if the Jacobian matrix $J(\mathbf{x_0})$ has n eigenvalues with negative real parts and p eigenvalues with positive real parts.

Theorem 2.2 *If $R_1 > 1$, $R_2 > 1$ and $k_1 < k_{1_{max}}$ then:*

1. *The equilibrium $\mathcal{A}_1$ is a saddle of type 2-2;*

2. *The equilibrium $\mathcal{A}_2$ is a saddle of type 3-1;*

3. *The equilibrium $\mathcal{A}_3$ is a saddle of type 3-1.*

Proof. From (9) the eigenvalues of $J(\mathcal{A}_1)$ are given by

$$\begin{aligned}
\lambda_1 = &\ -\tfrac{1}{2}(\alpha_1+\beta_1+\mu_1)+\tfrac{1}{2}\sqrt{(\alpha_1+\beta_1+\mu_1)^2+4\alpha_1\phi_1[1-\tfrac{1}{R_1}]},\\
\lambda_2 = &\ -\tfrac{1}{2}(\alpha_1+\beta_1+\mu_1)-\tfrac{1}{2}\sqrt{(\alpha_1+\beta_1+\mu_1)^2+4\alpha_1\phi_1[1-\tfrac{1}{R_1}]},\\
\lambda_3 = &\ -\tfrac{1}{2}(\alpha_2+\beta_2+\mu_2)+\tfrac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2+4\alpha_2\phi_2[1-\tfrac{1}{R_2}]},\\
\lambda_4 = &\ -\tfrac{1}{2}(\alpha_2+\beta_2+\mu_2)-\tfrac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2+4\alpha_2\phi_2[1-\tfrac{1}{R_2}]},
\end{aligned}$$

and satisfy: $\lambda_1>0$, $\lambda_2<0$, $\lambda_3>0$ and $\lambda_4<0$. This proves the first assertion.

From (9) the eigenvalues of $J(\mathcal{A}_2)$ are given by

$$\begin{aligned}
\lambda_1 = &-\frac{1}{2}(\alpha_1+\beta_1+\mu_1)+\frac{1}{2}\sqrt{(\alpha_1+\beta_1+\mu_1)^2-4\alpha_1\phi_1[1-\frac{1}{R_1}]},\\
\lambda_2 = &-\frac{1}{2}(\alpha_1+\beta_1+\mu_1)-\frac{1}{2}\sqrt{(\alpha_1+\beta_1+\mu_1)^2-4\alpha_1\phi_1[1-\frac{1}{R_1}]},\\
\lambda_3 = &\ -\tfrac{1}{2}(\alpha_2+\beta_2+\mu_2)+\\
&\ \tfrac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2+4\alpha_2\phi_2[1-\tfrac{1}{R_2}]+4\tfrac{c_1\alpha_2\mu_1}{\alpha_1}[1-\tfrac{1}{R_1}]k_2},\\
\lambda_4 = &\ -\tfrac{1}{2}(\alpha_2+\beta_2+\mu_2)-\\
&\ \tfrac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2+4\alpha_2\phi_2[1-\tfrac{1}{R_2}]+4\tfrac{c_1\alpha_2\mu_1}{\alpha_1}[1-\tfrac{1}{R_1}]k_2}.
\end{aligned}$$

Is immediate to see that $\lambda_3>0$ and $\lambda_4<0$. If

$$\phi_1>\frac{1}{4\alpha_1}[(\alpha_1+\beta_1+\mu_1)^2+4\mu_1(\alpha_1+\beta_1)]$$

then λ_1 and λ_2 are complex with negative real parts and if

$$\phi_1\le\frac{1}{4\alpha_1}[(\alpha_1+\beta_1+\mu_1)^2+4\mu_1(\alpha_1+\beta_1)]$$

then $\lambda_1<0$ and $\lambda_2<0$. This proves the second assertion.

From (9) the eigenvalues of $J(\mathcal{A}_3)$ are given by

$$\begin{aligned}
\lambda_1 = & -\tfrac{1}{2}(\alpha_1+\beta_1+\mu_1+c_2k_1[1-\tfrac{1}{R_2}])+ \\
& \tfrac{1}{2}\sqrt{(\alpha_1+\beta_1-\mu_1+c_2k_1[1-\tfrac{1}{R_2}])^2+4\alpha_1\phi_1}, \\
\lambda_2 = & -\tfrac{1}{2}(\alpha_1+\beta_1+\mu_1+c_2k_1[1-\tfrac{1}{R_2}])- \\
& \tfrac{1}{2}\sqrt{(\alpha_1+\beta_1-\mu_1+c_2k_1[1-\tfrac{1}{R_2}])^2+4\alpha_1\phi_1},
\end{aligned}$$

$$\lambda_3 = -\frac{1}{2}(\alpha_2+\beta_2+\mu_2)+\frac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2-4\alpha_2\phi_2[1-\frac{1}{R_2}]},$$

$$\lambda_4 = -\frac{1}{2}(\alpha_2+\beta_2+\mu_2)-\frac{1}{2}\sqrt{(\alpha_2+\beta_2+\mu_2)^2-4\alpha_2\phi_2[1-\frac{1}{R_2}]}.$$

It follows that $\lambda_1 > 0$, $\lambda_2 < 0$. If

$$\phi_2 > \frac{1}{4\alpha_2}[(\alpha_2+\beta_2+\mu_2)^2+4\mu_2(\alpha_2+\beta_2)]$$

then λ_3 and λ_4 are complex with negative real parts and if

$$\phi_2 \leq \frac{1}{4\alpha_2}[(\alpha_2+\beta_2+\mu_2)^2+4\mu_2(\alpha_2+\beta_2)]$$

then $\lambda_3 < 0$ and $\lambda_4 < 0$. This proves the last assertion.

■

For the sake of completeness we state the following lemma which is a particular case of the Theorem of Routh–Hurwitz. See [8], p. 62.

Lemma 2.3 *The polynomial $L(\lambda) = a_0\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4$, $a_0 > 0$, with real coefficients has all roots with negative real parts if and only if the numbers a_1, a_2, a_3, a_4 are positive and the inequality*

$$\Delta = a_1\ a_2\ a_3 - a_0\ a_3^2 - a_1^2\ a_4 > 0$$

is satisfied.

Theorem 2.4 *If $R_1 > 1$, $R_2 > 1$ and $k_1 < k_{1_{max}}$ then all the coefficients of the characteristic polynomial of $J(\mathcal{A}_4)$ are positive. Therefore, if*

$$\Delta = a_1\, a_2\, a_3 - a_3^2 - a_1^2\, a_4 > 0, \tag{10}$$

where

$$a_1 = \alpha_1 + \beta_1 + \mu_1 + \alpha_2 + \beta_2 + \mu_2 + k_1 G_4,$$

$$a_2 = \frac{\alpha_1 \phi_1}{c_1} M_4 + \frac{\alpha_2 \phi_2}{c_2} G_4 + (\alpha_1 + \beta_1 + \mu_1 + k_1 G_4)(\alpha_2 + \beta_2 + \mu_2),$$

$$a_3 = (\alpha_1 + \beta_1 + \mu_1 + k_1 G_4)\frac{\alpha_2 \phi_2}{c_2} G_4 + (\alpha_2 + \beta_2 + \mu_2)\frac{\alpha_1 \phi_1}{c_1} M_4 + \alpha_2 k_1 k_2 P_4 G_4,$$

$$a_4 = \alpha_2 \alpha_1 \phi_1 \left(k_2 \left(1 - \frac{1}{R_1}\right) P_4 + \frac{\phi_2}{c_1}\left(1 - \frac{1}{R_2}\right) M_4 \right),$$

then the differential equations (1) have an asymptotically stable equilibrium point at $\mathcal{A}_4$. If

$$\Delta < 0$$

then $\mathcal{A}_4$ is unstable.

Proof. From (9) the characteristic polynomial of $J(\mathcal{A}_4)$ is given by

$$[\lambda^2 + (\alpha_1 + \beta_1 + \mu_1 + k_1 G_4)\lambda + \frac{\alpha_1 \phi_1}{c_1} M_4][\lambda^2 + (\alpha_2 + \beta_2 + \mu_2)\lambda + \frac{\alpha_2 \phi_2}{c_2} G_4]$$
$$+\alpha_2 \mu_1 k_1 k_2 P_4 G_4 + \alpha_2 k_1 k_2 P_4 G_4 \lambda,$$

which can be written as

$$\lambda^4 + \lambda^3[\alpha_1 + \beta_1 + \mu_1 + \alpha_2 + \beta_2 + \mu_2 + k_1 G_4]$$

$$+\lambda^2[\tfrac{\alpha_1 \phi_1}{c_1} M_4 + \tfrac{\alpha_2 \phi_2}{c_2} G_4 + (\alpha_1 + \beta_1 + \mu_1 + k_1 G_4)(\alpha_2 + \beta_2 + \mu_2)]$$

$$+\lambda[(\alpha_1 + \beta_1 + \mu_1 + k_1 G_4)\tfrac{\alpha_2 \phi_2}{c_2} G_4 + (\alpha_2 + \beta_2 + \mu_2)\tfrac{\alpha_1 \phi_1}{c_1} M_4 + \alpha_2 k_1 k_2 P_4 G_4]$$

$$+\tfrac{\alpha_1 \phi_1}{c_1} M_4 \tfrac{\alpha_2 \phi_2}{c_2} G_4 + \alpha_2 \mu_1 k_1 k_2 P_4 G_4.$$

Now it is simple to see that the coefficients of the characteristic polynomial are given by a_1, a_2, a_3, a_4 above. From the hypotheses these coefficients are positive. The stability at $\mathcal{A}_4$ follows from Lemma 2.3.

$\blacksquare$

The following corollary is immediate from the fact that $a_i > 0$.

Corollary 2.5 *The Jacobian matrix $J(\mathcal{A}_4)$ has a pair of complex eigenvalues with zero real part if and only if*

$$a_3^2 - a_1\, a_2\, a_3 + a_1^2\, a_4 = 0, \tag{11}$$

where a_i are defined in Theorem 2.4.

In next section we study the stability of $\mathcal{A}_4$ under the condition (11), complementary to the range of validity of Theorem 2.4.

3 Hopf Bifurcation Analysis

3.1 Generalities on Hopf Bifurcations

The study outlined below is based on the approach found in the book of Kuznetsov [9], pp 175-178.

Consider the differential equations

$$\mathbf{x}' = f(\mathbf{x}, \mu), \tag{12}$$

where $\mathbf{x} \in \mathbb{R}^4$ and $\mu \in \mathbb{R}^m$ is a vector of control parameters. Suppose (12) has an equilibrium point $\mathbf{x} = \mathbf{x_0}$ at $\mu = \mu_\mathbf{0}$ and represent

$$F(\mathbf{x}) = f(\mathbf{x}, \mu_\mathbf{0}) \tag{13}$$

as

$$F(\mathbf{x}) = A\mathbf{x} + \frac{1}{2}\, B(\mathbf{x}, \mathbf{x}) + \frac{1}{6}\, C(\mathbf{x}, \mathbf{x}, \mathbf{x}) + O(||\mathbf{x}||^4), \tag{14}$$

where $A = f_\mathbf{x}(0, \mu_\mathbf{0})$ and

$$B_i(\mathbf{x}, \mathbf{y}) = \sum_{j,k=1}^{4} \frac{\partial^2 F_i(\xi)}{\partial \xi_j\, \partial \xi_k}\Big|_{\xi=0} x_j\, y_k, \tag{15}$$

$$C_i(\mathbf{x}, \mathbf{y}, \mathbf{z}) = \sum_{j,k,l=1}^{4} \frac{\partial^3 F_i(\xi)}{\partial \xi_j \, \partial \xi_k \, \partial \xi_l}\Big|_{\xi=0} x_j \, y_k \, z_l, \tag{16}$$

for $i = 1, 2, 3, 4$. Here the variable $\mathbf{x} - \mathbf{x_0}$ is also denoted by $\mathbf{x}$.

Suppose $(\mathbf{x_0}, \mu_\mathbf{0})$ is an equilibrium point of (12) where the Jacobian matrix A has a pair of purely imaginary eigenvalues $\lambda_{3,4} = \pm i\omega_0$, $\omega_0 > 0$, and no other critical (i.e., on the imaginary axis) eigenvalues.

Let $p, q \in \mathbb{C}^4$ be vectors such that

$$Aq = i\omega_0 \, q, \;\; A^\top p = -i\omega_0 \, p, \;\; \langle p, q \rangle = \sum_{i=1}^{4} \bar{p}_i \, q_i \;\; = 1. \tag{17}$$

The two dimensional center manifold can be parameterized by $w \in \mathbb{R}^2 = \mathbb{C}$, by means of $\mathbf{x} = H(w, \bar{w})$, which is written as

$$H(w, \bar{w}) = wq + \bar{w}\bar{q} + \sum_{2 \le j+k \le 3} \frac{1}{j!k!} \, h_{jk} w^j \bar{w}^k + O(|w|^4),$$

with $h_{jk} \in \mathbb{C}^4$, $h_{jk} = \bar{h}_{kj}$.

Substituting these expressions into (12) and (14) one has

$$H_w(w, \bar{w})w' + H_{\bar{w}}(w, \bar{w})\bar{w}' = F(H(w, \bar{w})). \tag{18}$$

The complex vectors h_{ij} are to be determined so that equation (18) writes as follows

$$w' = i\omega_0 w + \frac{1}{2} \, G_{21} w |w|^2 + O(|w|^4),$$

with $G_{21} \in \mathbb{C}$.

Solving the linear system obtained by expanding (18), the coefficients of the quadratic terms of (13) lead to

$$h_{11} = -A^{-1} B(q, \bar{q}), \tag{19}$$

$$h_{20} = (2i\omega_0 I_4 - A)^{-1} B(q, q), \tag{20}$$

where I_4 is the unit 4×4 matrix.

The coefficients of the cubic terms are also uniquely calculated, except for the term $w^2\bar{w}$, whose coefficient satisfies a singular system for h_{21}

$$(i\omega_0 I_4 - A)h_{21} = C(q,q,\bar{q}) + B(\bar{q},h_{20}) + 2B(q,h_{11}) - G_{21}q, \qquad (21)$$

which has a solution if and only if

$$\langle p, C(q,q,\bar{q}) + B(\bar{q},h_{20}) + 2B(q,h_{11}) - G_{21}q\rangle = 0.$$

Therefore

$$G_{21} = \langle p, C(q,q,\bar{q}) + B(\bar{q},(2i\omega_0 I_4 - A)^{-1}B(q,q)) - 2B(q, A^{-1}B(q,\bar{q}))\rangle, \quad (22)$$

and the *first Lyapunov coefficient* l_1 – which decides by the analysis of third order terms at the equilibrium its stability, if negative, or instability, if positive – is defined by

$$l_1 = \frac{1}{2\,\omega_0}\,\mathrm{Re}\,G_{21}. \qquad (23)$$

A *Hopf point* $(\mathbf{x_0},\boldsymbol{\mu_0})$ is an equilibrium point of (12) where the Jacobian matrix A has a pair of purely imaginary eigenvalues $\lambda_{3,4} = \pm i\omega_0$, $\omega_0 > 0$, and no other critical eigenvalues. At a Hopf point, a two dimensional center manifold is well-defined, which is invariant under the flow generated by (12) and can be smoothly continued to nearby parameter values.

A Hopf point is called *transversal* if the curves of complex eigenvalues cross the imaginary axis with non-zero derivative.

In a neighborhood of a transversal Hopf point with $l_1 \neq 0$ the dynamic behavior of the system (12), reduced to the family of parameter-dependent continuations of the center manifold, is orbitally topologically equivalent to the complex normal form

$$w' = (\gamma + i\omega)w + l_1 w|w|^2, \qquad (24)$$

$w \in \mathbb{C}$, γ, ω and l_1 are smooth continuations of 0, ω_0 and the first Lyapunov coefficient at the Hopf point [9], respectively. When $l_1 < 0$ ($l_1 > 0$) a family of stable (unstable) periodic orbits can be found on this family of center manifolds, shrinking to the equilibrium point at the Hopf point.

3.2 Hopf Bifurcation in the Biological Model

In this subsection we analyze the stability at $\mathcal{A}_4$ given by (6) under the condition (11). From (12) write the Taylor expansion (14) of $f(\mathbf{x})$. Thus

$$A = \begin{pmatrix} -(\alpha_1+\beta_1)-k_1G_4 & \phi_1(1-\frac{2M_4}{c_1}) & 0 & -k_1P_4 \\ \alpha_1 & -\mu_1 & 0 & 0 \\ k_2G_4 & 0 & -(\alpha_2+\beta_2) & \phi_2(1-\frac{2G_4}{c_2})+k_2P_4 \\ 0 & 0 & \alpha_2 & -\mu_2 \end{pmatrix} \tag{25}$$

and, with the notation in (14) to (16), one has

$$F(\mathbf{x}) \,-\, A\mathbf{x} = \left(-\frac{\phi_1 M^2}{c_1} - k_1PG, 0, -\frac{\phi_2 G^2}{c_2} + k_2PG, 0\right). \tag{26}$$

From (14), (15), (16) and (26) one has

$$B(\mathbf{x},\mathbf{y}) = (B_1(\mathbf{x},\mathbf{y}), 0, B_3(\mathbf{x},\mathbf{y}), 0)\,, \tag{27}$$

where

$$B_1(\mathbf{x},\mathbf{y}) = -\frac{2\phi_1}{c_1}\, x_2\, y_2 - k_1(x_1\, y_4 + x_4\, y_1),$$
$$B_3(\mathbf{x},\mathbf{y}) = -\frac{2\phi_2}{c_2}\, x_4\, y_4 + k_2(x_1\, y_4 + x_4\, y_1),$$

and

$$C(\mathbf{x},\mathbf{y},\mathbf{z}) \equiv 0. \tag{28}$$

To pursue the analysis consider the following table of specific parameters

$\alpha_1 = 0.7$	$\beta_1 = 0.003$	$\mu_1 = 0.6$	$\phi_1 = 2.3$	$c_1 = 400000$
$\alpha_2 = 0.3$	$\beta_2 = 0.0015$	$\mu_2 = 0.4$	$\phi_2 = 4$	$c_2 = 100$

(29)

taken from [7] and [3], where their biological feasibility in Brazilian fields is discussed.

With the above parameter values the differential equations (1) are in fact a two parameter system of differential equations where the parameters are k_1 and k_2 and can be written equivalently as

$$\mathbf{x}' = f(\mathbf{x}, k_1, k_2), \tag{30}$$

with $f(\mathbf{x}, k_1, k_2)$ defined by the right-hand sides of (1).

With the parameter values of table (29), the equilibrium point $\mathcal{A}_4$ (6) has the following coordinates

$$P_4 = \frac{800000\ (1.425 - 64.764\ k_1)}{4.508 + 1.444 \cdot 10^7\ k_1\ k_2},\ M_4 = \frac{933333.333\ (1.425 - 64.764\ k_1)}{4.508 + 1.444 \cdot 10^7\ k_1\ k_2},$$

$$L_4 = \frac{444.444\ (1.216 + 85550.400\ k_2)}{4.508 + 1.444 \cdot 10^7\ k_1\ k_2},\ G_4 = \frac{333.333\ (1.216 + 85550.400\ k_2)}{4.508 + 1.444 \cdot 10^7\ k_1\ k_2},$$

while R_1, R_2 and $k_{1_{max}}$, given by (2) and (7), have the form

$$R_1 = 3.81697,\ \ R_2 = 9.95025,\ \ k_{1_{max}} = 0.0220159. \qquad (31)$$

From the above equation and the Remark 1.1, the set of admissible parameters is given by (see Fig 1)

$$\mathcal{S} = \{(k_1, k_2) |\ 0 < k_1 < k_{1_{max}} = 0.0220159 \text{ and } 0 < k_2 \leq k_1\}. \qquad (32)$$

In this set $\mathcal{S}$ the curve $\Sigma = \Delta^{-1}(0)$ is well-defined (see (11)), where Δ is given by

$$\begin{aligned}&1699.422 - 233762.372k_1 - 6.860 \cdot 10^7 k_2 - 1.114 \cdot 10^7 k_1^2 - 2.175 \cdot 10^{12} k_2^2 - \\ &\quad 4.994 \cdot 10^{10} k_1 k_2 - 2.147 \cdot 10^8 k_1^3 - 4.079 \cdot 10^{12} k_1^2 k_2 - 1.529 \cdot 10^{15} k_1 k_2^2 - \\ &\quad 7.809 \cdot 10^{13} k_1^3 k_2 - 4.319 \cdot 10^{17} k_1^2 k_2^2 - 1.540 \cdot 10^{19} k_1 k_2^3 - 4.755 \cdot 10^{14} k_1^4 k_2 - \\ &\quad 1.752 \cdot 10^{19} k_1^3 k_2^2 - 6.741 \cdot 10^{21} k_1^2 k_2^3 + 2.940 \cdot 10^{18} k_1^4 k_2^2 - 1.703 \cdot 10^{24} k_1^3 k_2^3 + \\ &\quad 1.634 \cdot 10^{26} k_1^2 k_2^4 + 6.618 \cdot 10^{24} k_1^4 k_2^3 - 4.437 \cdot 10^{28} k_1^3 k_2^4 + 1.643 \cdot 10^{29} k_1^4 k_2^4,\end{aligned}$$

representing the parameters where $J(\mathcal{A}_4)$ has a pair of purely imaginary eigenvalues $\lambda_{3,4} = \pm i\omega_0$ with

$$\begin{aligned}\omega_0 = 1.2909\Big[&0.6909 + \frac{0.0071(-2.6479 \cdot 10^{-6} + k_2)(1.4219 \cdot 10^{-5} + k_2)}{k_2(3.1305 \cdot 10^{-7} + k_1 k_2)} + \\ &\frac{8.5745 \cdot 10^{-7}}{k_2} + \Big(\frac{1}{(6.2611 \cdot 10^{-7} + k_1 k_2) k_1 k_2}\Big((1.0783 \cdot 10^{-9} + \\ &5.0825 \cdot 10^{-5} k_2) k_2 - 3.1286 \cdot 10^{-4}(1.3649 \cdot 10^{-3} k_2)(6.0127 \cdot 10^{-6} + k_2) + \\ &0.9391\ k_1^2 (9.5980 \cdot 10^{-8} + k_2)(8.1563 \cdot 10^{-6} + k_2)\Big)\Big)^{1/2}\Big]^{1/2}.\end{aligned} \qquad (33)$$

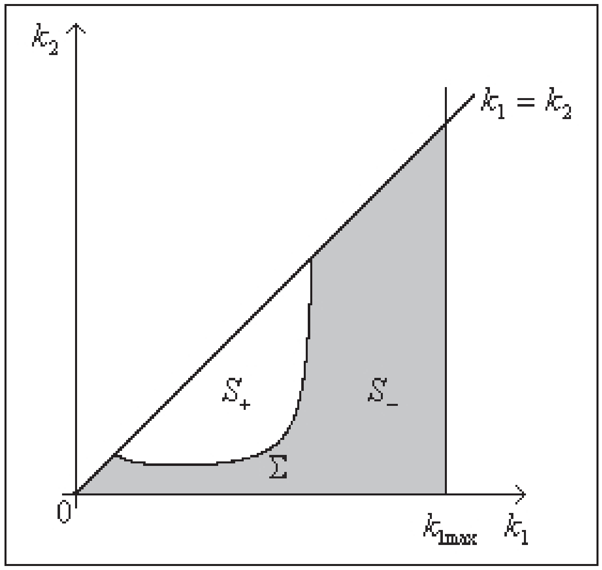

Figure 1: Set of admissible parameters $\mathcal{S}$ and Hopf curve Σ.

Thus one has (see Fig. 1)

$$\mathcal{S} = \mathcal{S}_+ \cup \Sigma \cup \mathcal{S}_-.$$

For parameter values in the region $\mathcal{S}_+$ the equilibrium $\mathcal{A}_4$ is unstable since the Jacobian matrix $J(\mathcal{A}_4)$ has two complex eigenvalues with positive real parts and two other real negative eigenvalues. For parameter values in the region $\mathcal{S}_-$ the equilibrium $\mathcal{A}_4$ is asymptotically stable since $J(\mathcal{A}_4)$ has two complex eigenvalues with negative real parts and two other real negative eigenvalues. The curve Σ is the curve of admissible parameters where the equilibrium $\mathcal{A}_4$ is a Hopf point.

Theorem 3.1 *Consider the differential equations (1) with the parameters given in the table (29). If $(k_1, k_2) \in \Sigma$ then the two parameter family of differential equations (1) has a transversal Hopf point at $\mathcal{A}_4$. This Hopf point at $\mathcal{A}_4$ is unstable and for each $(k_1, k_2) \in \mathcal{S}_-$, but close to Σ, there exists an unstable periodic orbit near the asymptotically stable equilibrium point $\mathcal{A}_4$. See Fig 1.*

Computer Assisted Proof. The proof follows the steps outlined in Subsection 3.1. However, all the expressions in the proof are too long to be put in print. For this reason, in the site [10] have been posted the main steps of the long calculations involved in the proof. This has been done in the form of a *notebook* for MATHEMATICA 5 [11]. A sufficient condition for being a Hopf point is that the first Lyapunov coefficient $l_1 \neq 0$. In fact, it can be shown numerically that $l_1(k_1, k_2) > 0$ for all values $(k_1, k_2) \in \Sigma$. A particular case and other related calculations are considered below for the sake of illustration.

Take the particular point $Q = (k_1 = 0.00331, k_2 = 0.00100) \in \Sigma$ with five decimal round-off coordinates [7]. For these values of the parameters

$$\mathcal{A}_4 = (18543.57758, 21634.17385, 738.0525862, 553.5394397).$$

The Jacobian matrix $J(\mathcal{A}_4)$ has eigenvalues

$$\lambda_1 = -3.61058,\ \lambda_2 = -0.22912,\ \lambda_{3,4} = \pm 2.84670i,$$

and thus

$$\omega_0 = 2.84670. \tag{34}$$

From (17) the eigenvectors q and p have the form

$$q = \begin{pmatrix} 820.5542609 + 1080.774610i \\ 295.1756045 - 139.5588184i \\ 862.8021803 + 130.4940530i \\ 26.01486634 - 87.27100717i \end{pmatrix},$$

$$p = \begin{pmatrix} 0.00003314748646 + 0.00006274424412i \\ -0.00003846764141 + 0.00003199241887i \\ 0.0005233172006 + 0.00007678211168i \\ 0.001254520214 - 0.004888597529i \end{pmatrix}.$$

One has

$$B(q, q) = \begin{pmatrix} -767.7418261 + 289.3499796i \\ 0 \\ 786.4902302 + 276.2661945i \\ 0 \end{pmatrix}$$

and

$$B(q,\bar{q}) = \begin{pmatrix} 482.6477605 \\ 0 \\ -809.3875158 + 0.6 \cdot 10^{-7} i \\ 0 \end{pmatrix}.$$

From (19) and (20) the complex vectors h_{11} and h_{20} have the form

$$-h_{11} = \begin{pmatrix} -1622.977370 + 0.9904140546 \cdot 10^{-7} i \\ -1893.473598 + 0.1155483063 \cdot 10^{-6} i \\ -5.359116331 - 0.3117318364 \cdot 10^{-9} i \\ -4.019337253 - 0.2337988771 \cdot 10^{-9} i \end{pmatrix},$$

$$h_{20} = \begin{pmatrix} 71.87520338 + 68.12253398 i \\ 9.204672581 - 7.866965075 i \\ 83.57142169 - 174.4554220 i \\ -8.839482676 - 5.024621730 i \end{pmatrix}.$$

From (22) the complex number G_{21} is given by

$$G_{21} = 0.057297 - 0.027485 i, \tag{35}$$

and from (23), (34) and (35) one has the first Lyapunov coefficient at Q

$$l_1(Q) = 0.00353522 > 0. \tag{36}$$

The above calculations have also been checked with 10 decimals round-off precision performed using the software MATHEMATICA 5 [11]. See [10].

Some other values of pairs $(k_1, k_2) \in \Sigma$, the values of the complex eigenvalues of $J(\mathcal{A}_4)$ as well as the corresponding values of $l_1(k_1, k_2)$ are listed the table below. The calculations leading to these values can be found in [10].

k_1	k_2	complex eigenvalues of $J(\mathcal{A}_4)$	$l_1(k_1, k_2)$
0.0004813	0.0004812	$\pm 4.76456i$	$4.69457 \cdot 10^{-8}$
0.0007954	0.0003535	$\pm 3.98051i$	$1.21597 \cdot 10^{-7}$
0.0011096	0.0003086	$\pm 3.59051i$	$2.17614 \cdot 10^{-7}$
0.0014238	0.0002950	$\pm 3.35518i$	$3.29018 \cdot 10^{-7}$
0.0017379	0.0003001	$\pm 3.19780i$	$4.52683 \cdot 10^{-7}$
0.0020521	0.0003220	$\pm 3.08560i$	$5.86835 \cdot 10^{-7}$
0.0023663	0.0003649	$\pm 3.00207i$	$7.30346 \cdot 10^{-7}$
0.0026804	0.0004427	$\pm 2.93795i$	$8.82421 \cdot 10^{-7}$
0.0029946	0.0005957	$\pm 2.88762i$	$1.04245 \cdot 10^{-6}$
0.0033088	0.0009855	$\pm 2.84745i$	$1.20994 \cdot 10^{-6}$
0.0036230	0.0035924	$\pm 2.81501i$	$1.38449 \cdot 10^{-6}$

■

Remark 3.2 *The value of the first Lyapunov coefficient l_1 does depend on the normalization of the eigenvectors q and p, while its sign is invariant under scaling of q and p obeying the relative normalization. See [9], p. 99. The values $l_1(Q)$ in (36) and $l_1(k_1, k_2)$ in the above Table are obtained with two different choices of the eigenvectors q and p, see [10]. This explains the difference in the order of magnitude of the numbers involved.*

As a consequence of Theorem 3.1 there are no Hopf points of codimension 2 on Σ since the sign of the first Lyapunov coefficient does not change. In Fig. 2 is illustrated the bifurcation diagram for a typical point on the curve Σ.

Assuming the same values in the table (29) in next theorem we study the behavior of the Hopf curve Σ in the set of admissible parameters $\mathcal{S}$ (see equation (32)) as the parameter c_2 increases. In fact, the carrying capacity, representing several other factors, has a determinant role on the populations under study.

Theorem 3.3 *The one parameter family of curves $\Sigma_{c_2} = \Delta_{c_2}^{-1}(0)$ has only one point of tangency T with the line $k_1 = k_2$ for $c_2 = 650.41463$. For values*

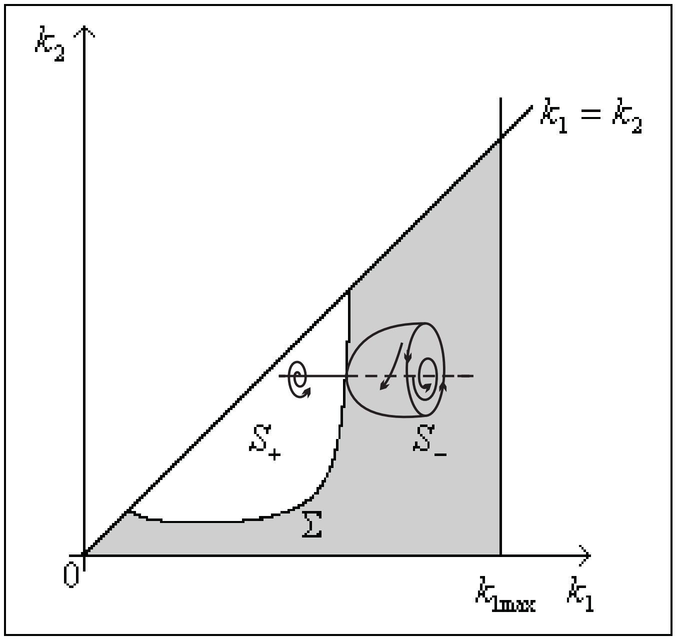

Figure 2: Bifurcation diagram for a typical point on the curve Σ.

$c_2 > 650.41463$ *the curve* Σ_{c_2} *does not intersect the set* $\mathcal{S}$*. Therefore for values* $c_2 > 650.41463$ *the set* $\mathcal{S}_+$ *is empty,* $\mathcal{S} = \mathcal{S}_-$ *and the equilibrium* $\mathcal{A}_4$ *is asymptotically stable for all values* $(k_1, k_2) \in \mathcal{S}$*. See Fig. 3.*

Proof. The surface of Hopf points, or equivalently the one parameter family of Hopf curves, where $J(\mathcal{A}_4)$ has a pair of purely imaginary eigenvalues is defined by $\Sigma_{c_2} = \{\Delta(k_1, k_2, c_2) = 0\}$ where $\Delta(k_1, k_2, c_2)$ (see (11)) is given by

$$
\begin{aligned}
&1699.422 - 2337.623c_2k_1 - 6.860 \cdot 10^7 k_2 - 1114.941c_2^2k_1^2 - 2.175 \cdot 10^{12}k_2^2 - \\
&4.994 \cdot 10^8 c_2k_1k_2 - 214.747c_2^3k_1^3 - 4.079 \cdot 10^8 c_2^2k_1^2k_2 - 1.529 \cdot 10^{13}c_2k_1k_2^2 - \\
&\quad 7.809 \cdot 10^7 c_2^3k_1^3k_2 - 4.319 \cdot 10^{13}c_2^2k_1^2k_2^2 - 1.540 \cdot 10^{17}c_2k_1k_2^3 - \\
&\quad 4.755 \cdot 10^6 c_2^4k_1^4k_2 - 1.752 \cdot 10^{13}c_2^3k_1^3k_2^2 - 6.741 \cdot 10^{17}c_2^2k_1^2k_2^3 + \\
&\quad 2.940 \cdot 10^{10}c_2^4k_1^4k_2^2 - 1.703 \cdot 10^{18}c_2^3k_1^3k_2^3 + 1.634 \cdot 10^{22}c_2^2k_1^2k_2^4 + \\
&\quad 6.618 \cdot 10^{16}c_2^4k_1^4k_2^3 - 4.437 \cdot 10^{22}c_2^3k_1^3k_2^4 + 1.643 \cdot 10^{21}c_2^4k_1^4k_2^4.
\end{aligned}
$$

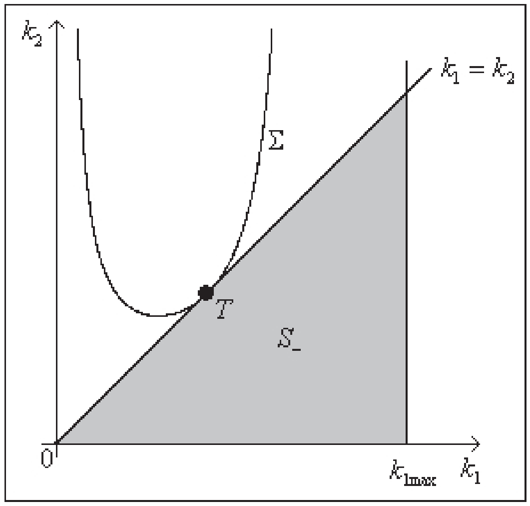

Figure 3: Curve Σ intersects $\mathcal{S}$ at one point T.

The intersection of the surface Σ_{c_2} with the plane $k_1 = k_2$ determines the curve $\mathcal{C}$, given implicitly by

$$N(k_1, c_2) = 1699.422 - (2337.623c_2 + 6.860 \cdot 10^7)k_1 - (1114.941c_2^2 + 2.175 \cdot 10^{12} + 4.994 \cdot 10^8 c_2)k_1^2 - (214.747c_2^3 + 4.079 \cdot 10^8 c_2^2 + 1.529 \cdot 10^{13} c_2)k_1^3 - (7.809 \cdot 10^7 c_2^3 + 4.319 \cdot 10^{13} c_2^2 + 1.540 \cdot 10^{17} c_2)k_1^4 - (4.755 \cdot 10^6 c_2^4 + 1.752 \cdot 10^{13} c_2^3 + 6.741 \cdot 10^{17} c_2^2)k_1^5 + (2.940 \cdot 10^{10} c_2^4 - 1.703 \cdot 10^{18} c_2^3 + 1.634 \cdot 10^{22} c_2^2)k_1^6 + (6.618 \cdot 10^{16} c_2^4 - 4.437 \cdot 10^{22} c_2^3)k_1^7 + 1.643 \cdot 10^{21} c_2^4 k_1^8 = 0.$$

Differentiating implicitly the above expression with respect to k_1 one has

$$\frac{dc_2}{dk_1} = -\frac{\frac{\partial N}{\partial k_1}}{\frac{\partial N}{\partial c_2}} = 0, \quad \frac{d^2 c_2}{dk_1^2} < 0,$$

at $k_1 = 0.00035$ and $c_2 = 650.41463$. Therefore the curve $\mathcal{C}$ is a graph near the point $(k_1 = 0.00035, c_2 = 650.41463)$ and has a local maximum point at $k_1 = 0.00035$. It can be shown [10] that this maximum is global since dc_2/dk_1 has no other zero. It is easy to verify through a calculation that the point

$T = (k_1, k_2) = (0.00035, 0.00035)$ belongs to Σ_{c_2} for $c_2 = 650.41463$. Now the gradient of Δ_{c_2} at T for $c_2 = 650.41463$ is given by

$$(-1.73746 \cdot 10^{10}, 1.73746 \cdot 10^{10}),$$

which is parallel to the vector $(-1, 1)$, the normal to the line $k_1 = k_2$.

■

Remark 3.4 *Since $k_{1_{max}}$ does depend on the parameter c_2, according to Eq. (7), so does the admissible region $\mathcal{S} = \mathcal{S}_{c_2}$. For $c_2 = 650.41463$, a calculation gives $k_{1_{max}} = 0.00338491$. This is compatible with position of T at $k_1 = k_2 = 0.00035$, as illustrated in Figure 3.*

4 Concluding Comments

In this paper we studied the system (1) of interest as a mathematical model for biological control, proposed by Yang and Ternes [1, 3, 2] and studied also by Santos [7]. Valuable field data are provided in [3], valid for the *citrus leafminer* and its native and imported enemies in the region of Limeira (São Paulo, Brazil). An extensive, enlightening discussion of the economic and agricultural interest of the problem, other pertinent differential equations models as well as extensive bibliography, are also presented there.

Under conditions made explicit in Remark 2.1 we determine the unique equilibrium point ($\mathcal{A}_4$) with positive coordinates and establish necessary and sufficient conditions for its (Lyapunov) stability (Theorem 2.4). It can be seen however that this condition $\Delta > 0$, when expressed in terms of the parameters is a rational function whose denominator does not vanish and its numerator is a polynomial of too many terms to be put in print, but still amenable to numerical calculations. For this reason the treatment of the stability of ($\mathcal{A}_4$) in Subsection 3.2 is computer assisted. The conclusion of this study, made precise in Theorem 3.1, is the existence of periodic orbits obtained by Hopf bifurcation, on the side (of $\Delta = 0$) where $\mathcal{A}_4$ is an attractor.

The study of the general analytic and geometric properties of the boundary of the stability region, given by the Hopf variety $\Delta = 0$, so as to include parameter values of biological interest as proposed here as well as others appearing in the work of Ternes [3], remain at the present moment as a mathematical challenge. Theorem 3.3 gives only a thin slice of the geometry.

The reports in [12] and [13], among many others, show that the interest for the combat of the *citrus leafminer* extends to most regions where citrus trees grow.

The Mathematica notebooks [10], with the table (29), used in the computer assisted arguments for the proofs of Theorems 3.1 and 3.3, can be adapted to tables with data pertinent to other geographic and climatic regions and involving different host–parasitoid interactions.

In [2] Ternes and Yang discuss, with pertinent documentation, the introduction of a foreign parasitoid, *Ageniaspis citricola* to add the native *Galeopsomya Fausta* in the combat with the *leafminer, Phyllocnistis citrella*. They propose a model with eight differential equations for the three species and their immature stages. In [2] and [3] are given starting steps for an analysis of the stability of the equilibria in this extended eight − dimensional system. Based in a numerical study of a complex equilibrium point they recommend that the biological control of the *leafminer* be implemented with both the native and foreign parasitoids. Meanwhile, the Hopf bifurcation analytic and computer algebra study of the complex equilibria of the eight equations, with the methods used in the present paper, seems unsurmountable at the present moment, due to the large number of parameters involved.

Acknowledgement: The first and second authors developed this work under the projects CNPq Grants 473824/04-3 and 473747/2006-5. The first author is fellow of CNPq. The fourth author is supported by CAPES. This work was finished while the second author visited Universitat Autònoma de Barcelona, supported by CNPq grant 210056/2006-1.

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